Wintering in the sun: niche partitioning by three nonbreeding *Pterodroma* petrel species in the equatorial Pacific Ocean

Running head: Niche partitioning by nonbreeding *Pterodroma* petrels

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Abstract

Niche divergence is expected for species that compete for shared resources, including migrants that occupy similar regions during the non-breeding season. Studies of temperate seabirds indicate that both spatial and behavioural segregation can be important mechanisms for reducing competition, but there have been few investigations of resource partitioning by closely-related taxa in low productivity, tropical environments. We investigated niche partitioning in three gadfly petrel taxa, *Pterodroma leucoptera leucoptera* (n = 22) , *P. leucoptera caledonica* (n = 7) and *P. pycrofti* (n = 12) during their non-breeding season in the eastern tropical Pacific Ocean by combining tracking data from geolocator-immersion loggers with remotely-sensed environmental data in species distribution models (SDMs), and by comparing feather stable isotope ratios. The three taxa showed spatial partitioning; two foraged in the North Equatorial Counter Current and one in the South Equatorial Current. This reflected differences in their realised habitat niches, with significant taxon-specific responses to thermocline depth, sea surface temperature and bathymetry. There were also differences among taxa in activity patterns, and all birds spent a much larger proportion of time in flight at night than during the day, suggesting predominance of nocturnal foraging behaviour. Comparison of stable isotope ratios in feathers suggests that *P. leucoptera leucoptera* and *P. pycrofti* mainly consume vertically-migrating mesopelagic fishes, whereas the diet of *P. leucoptera caledonica* also include some lower trophic level including crustaceans and squid. Unique insights can be gained from studies of the foraging ecology of tropical pelagic seabirds, in comparison with temperate and polar waters, and are urgently required for understanding and protecting tropical avifauna in key marine habitats

Introduction

The distribution of top predators in the marine environment is frequently linked to physical oceanographic processes that govern spatial and temporal variation in primary productivity and associated prey availability (Block et al. 2011). In particular, physical forcing in marine boundary currents creates convergence and upwelling zones known as some of the most productive marine environments on earth, where predators target and compete for prey concentrations that can be predictable at meso to large spatial scales (Belkin et al. 2009, Bost et al. 2009). Studies of seabird distribution during the breeding season demonstrate that populations minimise interspecific competition in such foraging zones through a variety of mechanisms including segregation in space and time, behaviour and diet (Phalan et al. 2007, Navarro et al. 2013, Moreno et al. in press). During the nonbreeding season, when seabirds are free from central-place foraging constraints, studies highlight the importance of spatial and dietary segregation, frequently across ecological gradients related to ocean temperature, reflecting the location of boundary systems (Spear et al. 2007, Thiebot et al. 2012, Cherel et al. 2013, Navarro et al. 2015, Quillfeldt et al. 2015).

Small gadfly *Pterodroma* petrels within the subgenus *cookilaria* (~ 10 species) are a group of seabirds that usually make long distance migrations during the non-breeding season to productive boundary systems in the temperate northern and southern Pacific Ocean where they exhibit both spatial and temporal resource partitioning (Rayner et al. 2011, Rayner et al. 2012, Priddel et al. 2014). However, not all *cookilaria* migrate to temperate habitats, with some species occupying tropical non-breeding habitats such as the eastern tropical Pacific Ocean (ETPO) (Kessler 2006), where they are part of a diverse seabird community (Au & Pitman 1986, Ballance et al. 1997, Spear et al. 2007, Priddel et al. 2014). Both theoretical (Pianka 1974) and empirical data (Torres 2009, Young et al. 2010) suggest that in such low productivity tropical habitats, competitors will increase niche separation to avoid competition. Accordingly, the community of *cookilaria* in the ETPO represents a distinctive ecological system for investigating niche partitioning in small Procellariiformes, providing a useful comparison with studies in temperate systems (Ainley et al. 1992, Navarro et al. 2015)

A number of gadfly petrels endemic to breeding sites in temperate Australasia are known, or considered likely, to occupy the ETPO during part of their seasonal cycle. Gould's Petrel (*Pterodroma leucoptera*; ~200–250 g) occurs as two subspecies with low levels of gene flow between populations breeding on islands off the coast of New South Wales, Australia (*P. leucoptera leucoptera*, hereafter *leucoptera*) and on the main island of New Caledonia (*P. leucoptera caledonica*, hereafter *caledonica*)(de Naurois 1978, Priddel et al. 1995, Gangloff 2010). During the nonbreeding season, both subspecies migrate to the ETPO (Priddel et al. 2014). Pycroft's petrel (*Pterodroma pycrofti*, hereafter *pycrofti*) is endemic to islands off the northeast coast of New Zealand (~130 –200 g (Marchant & Higgins 1990) but has a poorly known nonbreeding distribution that likely extends, in part, to the tropical Pacific (Spear et al. 1992). Recent genetic research indicates that *pycrofti* is a sister taxon to *leucoptera* and *caledonica* (Steeves et al in prep) presenting an opportunity for comparative analysis of foraging ecology in these morphologically and genetically similar taxa.

We investigated niche separation in *leucoptera*, *caledonica* and *pycrofti* during the nonbreeding season by combining tracking data from geolocator-immersion loggers with remotely-sensed environmental data in species distribution models (SDM), and by comparing stable isotope ratios in feathers grown by tracked individuals during the same period. Our aims were to present the first detailed analysis of the nonbreeding movements of individual *pycrofti* and to highlight differences in habitat use and foraging ecology indicative of niche partitioning among these three closely-related taxa.

Materials and Methods

Tracking data

Tracking methods for *leucoptera* and *caledonica* are provided by Priddel *et al.* (2014). In summary, combined geolocator-immersion loggers (MK14, British Antarctic Survey, Cambridge, UK and NanoLAT2900, Lotek, Ontario, Canada) were deployed on adult *leucoptera* (subspecies population size 800 – 1000 breeding pairs (Priddel & Carlile 2007)) at Cabbage Tree Island (Australia) on March 2010 and *caledonica* (subspecies population size 1000 – 10000 breeding pairs (Brooke 2004)) at Grande Terre (the main island of New Caledonia) in January 2010. Loggers were retrieved at both sites between November 2010 and January 2011 providing data on the entire nonbreeding period for 22 *leucoptera* and 7 *caledonica* respectively. Similar loggers (MK18, British Antarctic Survey, Cambridge, UK, 2g) were attached to twelve *pycrofti* (subspecies population size 2500 – 4000 breeding pairs (Brooke 2004)) at Red Mercury Island (New Zealand) in December 2009, and 10 (83%) were retrieved in January 2011, of which two failed to provide data. All loggers were attached using the methods described by Rayner et al. (2008) and weighed < 1.5% of adult body mass.

Light data from the loggers were processed following the methods of Rayner et al. (2012). The nonbreeding phase was defined according to Priddel et al. (2014) based on the first location outside or inside a 1000 km buffer (an arbitrary but standardised measure) around the colony at the end or start, respectively, of the breeding season. The loggers tested for saltwater immersion data every 3 s, with the data binned into ten minute intervals, resulting in values ranging from 0 (dry) to 200 (immersed for whole period). These data were analysed using the methods of Rayner et al. (2012), providing temporal data on percent of time immersed, flight bouts greater than 10 minutes, and duration of flight bouts during daylight and darkness (based on the timing of civil twilight) for each species.

Construction of species distribution models (SDM)

Post-processed geolocation data from each species during the nonbreeding season were included in binomial species distribution models (SDM) following methods presented in Torres et al. (2015). In brief, locations from tracked individuals of each species (*leucoptera* n = 22, *caledonica* n = 7, *pycrofti* n = 8) were used to construct monthly kernel density estimates (search radius 200 km) during the non-breeding season for all three species between April and October. Presence data for each SDM were those locations that fell within the 50% density contour for each of those months, which was considered to represent core habitat. Background data (otherwise known as pseudo-absences) implemented in the SDM for each month were uniformly-spaced locations (every 100 km^2) falling within the 90% density contour for all species locations (April through October; n = 6245). This method was based on the assumption that all habitat was equally available to the three taxa within the timeframe of their non-breeding phase. Background locations were randomly assigned dates between the date of arrival and departure for each species, and bird identity in proportion to the number of presence points from each bird. Using these background and presence data we produced binomial boosted regression tree (BRT)(Freidman 2001) models of presence-availability (Boyce et al. 2002, Torres et al. 2015) that describe the distribution of each *cookilaria* petrel relative to the available habitat across the entire tropical pacific region exploited by all species.

For each species model of presence-availability, a range of static and remotely-sensed environmental data were used to describe habitat use. Depth values at each presence and background point were extracted from the 30 arc-second General Bathymetric Chart of the World (http://www.gebco.net/; GEBCO). Seabed slope angle and minimum distance to land were derived from the GEBCO bathymetry data using the package 'raster' in R 3.1.1 (R Core Team 2014). Several dynamic oceanographic variables (Table 1) were obtained from NOAA ERDDAP web servers using the Xtractomatic routines in R (http://coastwatch.pfel.noaa.gov/xtracto/): Chlorophyll-a concentration (CHL; 8-day), Sea surface temperature (SST; 8-day), sea surface height deviation (SSH; 1-day), Ekman upwelling (EKM; 3-day) and wind speed (WIND; 3-day). We obtained gridded, annual climatology data (12 month) for top of thermocline depth from IFREMER (http://www.ifremer.fr/cerweb/deboyer/mld); selecting the appropriate monthly grids for the non-

breeding period. The median values obtained for these environmental variables were those within a 200km radius of each location. This extraction technique accounted for the potential 200+ km spatial error in geolocation data (Phillips et al. 2004). The absolute deviation of the dynamic variables were also included in the models to assess how environmental variability may influence petrel habitat and log transformations of slope, WIND, CHL and EKM were implemented in the models to account for skewed distributions.

SDMs of each petrel species were generated using BRT models, which has demonstrated strong predictive performance and model parsimony, including for another pelagic petrel species (Elith et al. 2006, Buston & Elith 2011, Torres et al. 2013, Torres et al. 2015). BRT is a machine learning method that can handle correlated, interacting and non-linear data, all of which are common in ecological studies (Leathwick et al. 2006, Elith et al. 2008). Two algorithms are applied in BRT modelling: the first partitions the predictor space into homogeneous response groups using decision trees, and the second boosts this process to iteratively optimize the predictive performance of the model (Elith et al. 2008). The process combines a large number of individual decision trees to generate a BRT model.

The contribution of each predictor variable to a BRT model is determined by the number of times it is used to split a tree branch. If a predictor variable contributed less than 5% to the model, the model was re-run without that variable (Buston & Elith 2011). The learning rate (lr) of a BRT determines the contribution of each fitted tree to the final model and was set at 0.0025, while the bag fraction, which is the proportion of samples used at each tree from the whole dataset, was set at 0.5. Tree complexity (tc), which represents the number of nodes on each tree and determines the number of interactions between predictors, was allowed to vary between 1 and 4 so that the number of boosting iterations, known as the number of trees (nt), was greater than 1000, as recommended by Elith et al. (2008). Each model dataset included multiple presence and background points from the same bird track, and with varying sample sizes; to account for this internal structure in the datasets, CV-folds were specified (De'ath 2007) as all presence and background locations from an individual bird. CV-folds withhold subsets of data from the model at each tree that are subsequently used to test model fit.

While generating each BRT, 10% of presence and 10% of background locations were withheld from model calibration for external validation to assess predictive performance and select optimal model parameters. Four metrics were used to select the optimal model and evaluate predictive performance: cross-validation deviance explained and area under the receiver operator curve (AUC) calculated during the modelling procedure, and by external validation metrics of deviance between observed and predicted values (validation deviance) and AUC (validation AUC) calculated using the withheld data. Due to the presence *vs.* availability design of the BRT models, k-fold cross validations (Boyce et al. 2002) were also conducted on the optimal models to assess the predictive capacity of 'used' locations, while ignoring the predictability of absence locations because these are less certain when working with background or pseudo-absence data (Torres et al. 2015). The k-fold cross validation binned the predicted habitat suitability of each presence and absence location into equal-interval groups between 0 and 1 (0-0.1, 0.1-0.2, 0.2-0.3, etc.), and the proportion of presence locations in each bin was determined. A Spearman-rank correlation (rs) was calculated between bin rank (0, 0.1. 0.2, 0.3, etc.) and the proportion of presence locations to assess whether the latter increased with increasing suitability of predicted habitat, indicating good predictive performance (Torres et al. 2015).

Stable isotope ratios

Observations of our study taxa indicate worn and fresh plumage at the end and beginning of each breeding season, consistent with previous research indicating that *cookilaria* moult occurs during nonbreeding when dietary signals are encorporated into new plumage (Marchant & Higgins 1990, Spear et al. 1992) (Hobson 1999). Stable isotope ratios of N ($\delta^{15}N$) and C ($\delta^{13}C$) provide an indication of both the trophic level and carbon source (benthic versus pelagic, inshore versus offshore, and information on water mass) of prey ingested during the time of tissue formation, which in the case of feathers from adult seabirds typically allows comparisons between trophic level and geographic segregation during the nonbreeding period (Hobson 1999, Phillips et al. 2009). To enable a comparison between stable isotope ratios and distribution from tracking data, a single body feather was collected from each *leucoptera* (n = 10), *caledonica* (n = 8) and *pycrofti* (n = 10) upon geolocator retrieval. Feathers were stored in plastic bags in the field. Once in the lab, feathers were cleaned with

70% ethanol, rinsed in distilled water to remove contaminants, dried in at 50°C and cut into very fine fragments. Stable isotope analyses of a subsample (~0.7 mg) of each homogenized feather were carried out at National Institute of Water & Atmospheric Research (NIWA) using an AS200_LS autosampler and NA 1500N (Fisons Instruments, Rodano, Italy) elemental analyser combustion furnace connected to a Delta^{Plus} continuous flow, IRMS (Thermo-Fischer Scientific, Bremen, Germany). Operational details are outlined in (Rayner et al. 2008) with the exception that $\delta^{13}C$ values were calibrated against CO_2 reference gas, relative to the international standard Carrara Marble NSB-19 (National Institute of Standards and Technology (NIST), Gaithersberg, MD, USA). This, in turn, was calibrated against the original Pee Dee Belemnite (PDB) limestone standard and was then corrected for ^{17}O. A two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{15}N$ = -4.52±0.12 ‰) and IAEA-N-2 (ammonium sulphate: certified $\delta^{15}N$ = +20.41 ±0.2 ‰) was applied to $\delta^{15}N$ data. Carbon isotope data were corrected via a two-point normalisation process using NIST 8573 (USGS40 L-glutamic acid; certified $\delta^{13}C$ = --26.39±0.09 ‰) and NIST 8542 (IAEA-CH-6 Sucrose; certified $\delta^{13}C$ = -10.45 ±0.07 ‰). DL-Leucine (DL-2-Amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, Lot 127H1084, Sigma, Australia) was run every 10 samples to check analytical precision and enable drift corrections to be made if necessary. Additional international standards NIST 8574 (USGS41 L-glutamic acid; certified $\delta^{13}C$ = +37.63 ±0.10 ‰ and $\delta^{15}N$ = +47.57 ±0.22 ‰), NIST 8547 (IAEA-N1 ammonium sulphate; certified $\delta^{15}N$ = +0.43 ±0.04) were run daily to check isotopic accuracy. Repeat analysis of standards produced data accurate to within 0.25 ‰ for both $\delta^{15}N$ and $\delta^{13}C$, and a precision of better than 0.32 ‰, for $\delta^{15}N$ and 0.24 ‰ $\delta^{13}C$.

Statistical analyses

Migration arrival and departure dates were compared between species using contingency analysis. Following tests for normality, a combination of non-parametric tests (Kruskall Wallace tests) and parametric tests (ANOVA) were used to test for differences among species in time spent within the non-breeding core range (50% kernel), activity parameters (based on the immersion data), and stable isotope ratios, respectively. Parametric and non-parametric multiple comparisons were used to test

249 for pairwise differences (Wilcoxon matched pairs and Tukey's pairwise comparisons) between
250 species. Analyses were conducted using JMP 11.2.0 (©SAS Institute 2013) with a threshold of
251 significance at $\alpha = 0.05$. Unless indicated otherwise, data are presented as mean ± SD. Geospatial
252 processing of geolocation data was conducted using ArcGIS v10.3 (ESRI, CA, USA). Extraction of
253 remote-sensing data, creation of static environmental variables and BRT modelling were conducted in
254 R 3.1.1 (R Development Core Team 2013) using the packages dismo (Hijmans et al. 2012), Raster
255 (Hijmans & van Etten 2012), Gbm, PresenceAbsence (Freeman 2007), and with custom code by Elith
256 et al. (2008).

Results

Processing of light data from *leucoptera* (n = 22 adults), *caledonica* (n = 7 adults) and *pycrofti* (n = 8 adults), provided a total of 5287, 2330 and 2965 locations, respectively, for SDM analyses. *Leucoptera*, *caledonica* and *pycrofti* exhibited spatial segregation in their core distributions within the central and eastern tropical Pacific Ocean, but there were no significant differences in migration timetables, including the time spent in core areas (Table 2). The core region used by *leucoptera* was from 10°N–5°S, 150–165°W, encompassing the eastern sector of the Republic of Kiribati (Line Islands), whereas that used by *caledonica* was 3000--6000 km southeast in the region of the East Pacific Rise (0 – 15°S, 135°- 100°W) (Figs. 1 and 2). Core areas of *pycrofti* were from 0-10°N, 140°-135°W in the eastern equatorial Pacific, and situated between those of *leucoptera* and *caledonica* (Fig. 1 and 2). The migration routes of *pycrofti* were similar to those of *leucoptera* and *caledonica* (Priddel et al 2014); all birds first migrated east from New Zealand (at approximately 40°S) and then north to reach their nonbreeding range, and the return (pre-breeding) migration was southwest through Melanesia to reach waters around their respective colony (Fig. 1).

Species distribution models

Optimal BRT models for each petrel species performed well according to internal validation metrics and external measures of predictive performance using the withheld data (Table 3). Four predictor variables were common to all three models: Thermocline, Depth, SST and Chl collectively contributed 79%, 74%, 68%, and 39%, respectively, to all three models (total contribution of 87%: 261/300% for all three models). All models had a tree complexity of two, allowing one interaction between terms. Species-environment response plots for these four variables indicate that each species used different habitats (Fig. 3). Intra-species comparisons showed that presence of *leucoptera* and *caledonica* peaked in habitats where the thermocline was reached at > 100 m, and both species exhibited a positive response to a deeper thermocline. Conversely, *pycrofti* showed a negative response to a deeper thermocline, with presence peaking in habitats with the thermocline at ~ 25 m (Fig. 3). Niche separation by depth was also evident, with *leucoptera* presence peaking in the deepest

283 regions (> 5000 m), *pycrofti* in habitats with water depths of 4-5,000 m, and *caledonica* in shallower
284 habitats (< 4000 m) (Fig. 3). *Leucoptera* presence peaked in habitats with the highest SST (27-29 ºC),
285 *pycrofti* at mid-temperatures (25-28 ºC), and *caledonica* in cooler waters (20 - 26 ºC) (Fig. 3). Overlap
286 in habitat preferences relative to Chl was apparent between *caledonica* and *pycrofti*, with both taxa
287 showing increased presence in waters with low Chl, whereas *leucoptera* avoided that habitat (Fig 3).

288 At-sea activity patterns

289 There were significant differences in flight activity between daylight and darkness in all three species;
290 tracked birds spent less time on the water and made more, and longer flight bouts in darkness (Table
291 5; pairwise tests at 0.01). There was no significant difference in the daylight activity patterns between
292 species; all three taxa spent a similar amount of time on the water ($F_{2, 20}$ = 2.16, P = 0.14), and the
293 number of flight bouts (P = 0.34), and flight bout duration (P = 0.42) were comparable (Fig. 4). In
294 contrast, during darkness, the time spent on the water by *pycrofti* was greater than in *leucoptera* and
295 *caledonica* (Pairwise Tukey tests P < 0.05 and P < 0.001), and by *leucoptera* was greater than in
296 *caledonica* (Tukey HSD P < 0.05) (Table 4, Fig. 4). The trend of higher night time activity by
297 *caledonica* was consistent with the significantly higher number of flight bouts and longer duration of
298 flight bouts during darkness than in *leucoptera* and *pycrofti* ($F_{2, 20}$ = 8.61, P < 0.01; $F_{2, 20}$ = 13.31, P <
299 0.001); these last two taxa did not differ significantly in the number (P = 0.18) or duration of flight
300 bouts (P = 0.06).

301 *Leucoptera* and *pycrofti* exhibited higher flight activity during daylight and darkness at the beginning
302 and ending of the nonbreeding period, with a reduction in activity in June to August (Fig. 4).
303 *Caledonica* showed similar activity patterns across the nonbreeding season during daylight hours,
304 whereas night time activity remained high from April to October (Fig. 4).

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Isotopic niche

Nitrogen isotope ratios differed significantly between the three species (Fig. 5; $F_{2, 27} = 19.52$, P < 0.001). $\delta^{15}N$ in feathers of p*ycrofti* (16.91 ± 1.67) and *leucoptera* (15.22 ± 1.67) did not differ significantly ($\delta^{15}N$ 16.91 ± 1.67 and $\delta^{15}N$ 15.22 ± 1.67 respectively; pairwise tukey test, p = 0.09), but were higher than that in *caledonica* (12.45 ± 0.93, Pairwise Tukey tests both $p < 0.01$) (Fig. 5). $\delta^{13}C$ in feathers of *caledonica* (-15.72 ± 0.55) were higher than in *leucoptera* (-16.43 ± 0.60) but not *pycrofti* (-16.04 ± 0.28) (Fig. 5, $F_{2, 27} = 4.93$, P < 0.01, Pairwise Tukey tests: *caledonica* - *leucoptera* (p <0.01), *caledonica* – *pycrofti* (P = 0.38), *leucoptera* - *pycrofti* (p = 0.18).

Discussion:

Pterodroma petrels are among the most wide-ranging of all birds, and capable of traversing >1,000 km within a single day (Pinet et al. 2011, Rayner et al. 2011, Rayner et al. 2012). Despite this capacity for long-distance travel and thus shared habitat use, our three study taxa showed clear differences in distribution and habitat use during the non-breeding season but not in the timing of movements to and from these habitats. The core distributions of *leucoptera* and *pycrofti* were separated longitudinally - west of ~ 158° W, and east of 133° W, respectively - within the North Equatorial Counter Current (NECC) (Fig. 2, C), extending south to the edge of the cooler South Equatorial Current (SEC)(2-5°N) and north to the North Equatorial Current (NEC)(12-14°N), whereas c*aledonica* was distributed mainly in the South Equatorial Current (SEC) (0 - 15°S) between 135°W and 95°W. The preference of *pycrofti* and *leucoptera* for the waters of the NECC is consistent with at-sea observations of a range of procellariiform species in this region, including *Puffinus newelli, Puffinus pacificus, Pseudobulweria rostrate* and other gadfly petrels, *Pterodroma cervicalis, Pterodroma externa* and *Pterodroma sandwichensis,* (Ballance et al. 1997, Spear et al. 2001). Previous studies have suggested that *leucoptera* associates with the SEC (Ribic et al. 1997). However, this previous supposition is inconsistent with our data, which indicated that the tracked *leucoptera* occupied strikingly different habitats to its sister taxon in the western NECC. This result reaffirms the utility of tracking studies for revealing population-specific foraging ranges for taxa that are similar morphologically, and therefore difficult to distinguish at sea (Rayner et al. 2011). Moreover, this utility is particularly relevant for *caledonica* and *leucoptera* with significantly different populations sizes (*caledonica* ~ 10 000 breeding pairs, *leucoptera* ~ 1000 breeding pairs; (Brooke 2004, Priddel & Carlile 2007), making it particularly important to determine foraging areas and ensure a balanced assessment of at-sea threats.

Large scale spatial segregation is an important component of resource partitioning by small procellariform seabirds at high latitudes, as demonstrated by recent studies linking divergent distributions with species-specific preferences for particular sea surface temperature regimes, frequently partitioned across oceanic fronts (Navarro et al. 2013, Navarro et al. 2015, Quillfeldt et al.

2015). The ETPO lacks the strong latitudinal gradients in temperature typical of higher latitude regions in the Southern Ocean. Instead, the SDMs for our study taxa indicate that spatial segregation was paralleled by subtle taxon-specific differences in habitat niche, across a range of environmental predictors.

Functional relationships with depth of the thermocline (reflecting a subsurface gradient in temperature below the warm surface mixed layer), SST and depth indicates a division into two strategies of habitat use by the three taxa; *leucoptera* and *pycrofti* foraged in deep and warm waters where the depth of the thermocline was the strongest predictor of presence yet where both species had opposing functional relationships with thermocline depth: *leucoptera* preferring a deeper thermocline and *pycrofti* a shallower one. There is evidence that in the ETPO, the thermocline depth is a strong predictor of the abundance and distribution of other seabirds (Ballance et al. 1997, Spear et al. 2001, Ballance et al. 2006). In the NECC, vertically-migrating prey aggregate at the top of the thermocline and are frequently driven to the surface by feeding tuna and dolphins and thus exploited by a range of diurnally-feeding seabirds (Ballance et al. 2006). *Leucoptera* and *pycrofti* in these habitats are solitary foragers and not considered parts of this tuna-dolphin-seabird feeding assemblage (Spear et al. 2007), yet their presence was nevertheless predicted strongly by thermocline depth, indicating that similar ecological processes influence their distribution. Conversely, the presence of *caledonica* in the SEC was associated with cooler SSTs and shallower waters, particularly over the east Pacific rise, where thermocline depth was a weak predictor. Bathymetric features associated with the east Pacific rise in this region likely provide foraging opportunities as a result of upwelling that are targeted by various *Pterodroma* species (Rayner et al. 2012).

In the ETPO low iron availability reduces primary production resulting in a low chla environment (Pennington et al. 2006). The responses of the tracked birds to chla gradients were weak and indicated the use of waters with generally uniform and low chla values, particularly by *leucoptera* and *pycrofti* which maintained core habitats in oligotrophic waters of the NECC. This result is inconsistent with the results of studies demonstrating spatial relationships between chla, prey and predators in the ETPO (Ballance et al. 2006) and at higher latitudes where chla is more abundant

(Weimerskirch 2007, Peron et al. 2010). The analysis of immersion data from the three study taxa showed a striking pattern of reduced time resting on the surface, more numerous and longer flight bouts and higher variance in activity parameters during darkness than daylight. These results suggest that although our study taxa may forage opportunistically during daylight, their primary foraging strategy in the ETPO is to exploit nocturnally available prey, which is consistent with previous research on tropical (Spear et al. 2007, Pinet et al. 2011, Ramirez et al. 2013)) and temperate procellariiform seabirds (Imber 1973, Imber 1996, Rayner et al. 2012). In a nine-year study (1983-1991), Spear et al (2007) demonstrated that the diet of small procellariform species in the ETPO, including *leucoptera*, was dominated (>90%) by vertically-migrating mesopelagic fishes that were not associated with diurnally feeding surface predators. Although our comparison of nitrogen stable isotope ratios in feathers grown during the nonbreeding period suggest little dietary segregation between *leucoptera* and *pycrofti*, which occupy waters north of the equatorial front and NECC, the mean δ^{15}N values in these two taxa were higher than in *caledonica*, which occupy habitats in the SEC. Values of 13 to 18‰ for δ^{15}N in *leucoptera* and *pycrofti* feathers indicates that the tracked birds were foraging at a similar trophic level to tropical piscivores (Young et al. 2010), confirming a diet likely dominated by mesopelagic fishes (myctophids, bregmacerotids, diretmids, and melamphaids)(Spear *et al*. 2007). In contrast, the lower δ^{15}N of *caledonica* (11.0 to 14.0‰) suggests the additional consumption of prey from lower trophic levels, such as cephalopods or marine crustaceans (δ^{15}N of 8.1 to 10.2‰, and 3.6 to 6.5‰,)(Quillfeldt et al. 2005). This interpretation assumes there are no differences in regional baselines for δ^{15}N, which is supported by the similarity in δ^{13}C values for all three study taxa, which is consistent with foraging in deep tropical waters within a narrow latitudinal range (Hobson et al. 1994, Young et al. 2010).

In conclusion, our study of three closely-related *Pterodroma* petrels in the ETPO is consistent with theoretical and empirical data on niche overlap, which predicts divergence in habitat use, diet or behaviour among competitors that are sympatric in low resource environments. The slight behavioural differences appear unlikely to reduce inter-specific competition given the high morphological similarities between the three taxa. Rather, competition appears to be avoided by

habitat segregation. The SDMs provide evidence that the spatial separation between these three taxa is driven by differences in realized habitat niches. However unlike temperate systems, where seabird distributions can be predicted by strong surface temperature, wind or productivity gradients, two of three of our species were present in oligotrophic waters north of the equator, and the overall distribution of our study taxa was mediated by subtle horizontal and vertical temperature gradients, as well as depth. Thermocline depth in particular was a strong predictor of presence, and its role appears linked to the unique foraging niche of the study taxa. All three taxa were highly active during darkness, and thermocline depth likely plays a critical role by governing the proximity to the surface of the key prey source, which are vertically-migrating mesopelagic fishes. The nocturnal foraging niche of the *Pterodroma* petrels parallels the diurnal tuna-dolphin-seabird assemblages that make use of shallow thermoclines in the same region (Spear et al. 2007). Our study highlights the unique insights that can be gained from comparative studies of foraging ecology between pelagic seabirds in tropical systems and temperate or polar waters, and reinforces the importance of the ETPO as a critical habitat for numerous small Procellariiformes that breed in temperate regions. Management programs seeking to protect key marine habitats for the many highly threatened temperate and tropical *Pterodromas* would benefit from further tracking to map foraging areas during the breeding and non-breeding seasons, and to identify oceanographic drivers and their impacts on distributions.

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424 legend”, Mr Vince Vaanders (23/03/1970 - 18/08/2013).

425 Table 1. Environmental variables used in construction of boosted regression tree models.

Variable (units)	**Product code**	**Temporal resolution**	**Spatial resolution (degrees)**	**Data source**
Sea Surface Temperature (°C)(SST)	TMHchla8day	8-day	0.05	MODIS AQUA www.oceancolor.org
Chlorophyll-*a* Concentration (mg/m^3)(Chl)	TMHsstd8day	8-day	0.05	MODIS AQUA www.oceancolor.org
Sea surface height deviation anomaly (m)(SSHD)	TTAsshd1day	1-day	0.25	DUAACS AVISO www.aviso.oceanobs.com
Wind speed (m/s)(Wind)	TQAumod3day	3-day	0.25	METOP ASCAT www.eumetsat.int
Ekman upwelling (m/day)	TQAwekm3day	3-day	0.25	METOP ASCAT www.eumetsat.int
Top of thermocline depth (m)		Monthly climatology	2	IFREMER http://www.ifremer.fr/cerweb/deboyer/mld
Depth (m)		Static	0.0083	GEBCO www.gebco.net
Seabed slope angle (°)(Slope)		Static (derived)	0.0083	GEBCO www.gebco.net
Distance to nearest land (km)		Static (derived)	0.0083	GEBCO www.gebco.net

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Table 2.Timing of arrival and departure in core nonbreeding habitats for *leucoptera*, *caledonica*, and *pycrofti* in the eastern tropical Pacific Ocean in 2010. P values indicate significance of contingency analysis to assess differences between species in arrival and departure dates, and time spent in core areas. Data are shown as means ± standard deviation in days, with range in parentheses.

	P. l. leucoptera	*P.l. caledonica*	*P. pycrofti*	P
Arrival nonbreeding habitat	24 Apr ± 9.8 days (7 Apr – 12 May) n = 14	18 May ± 13.0 days (4 May – 13 Jun) n = 7	21 Apr ± 12.35 days (5 Apr – 14May) n = 8	0.20
Departure nonbreeding habitat	14 Sep ± 18.7 days (15 Aug – 16 Oct) n = 9	4 Oct ± 23.5 days (31 Aug - 28 Oct) n = 7	5 Sep ± 4.24 days (2 Sept – 13 Sept) n = 5	0.51
Time in nonbreeding core	141.3 ± 17.6 days (113-161) n = 9	135.9 3 ± 31.1 days (78-174) n = 7	137.0 ± 16.6 days (110-152) n = 5	0.13

443 Table 3.Boosted regression tree (BRT) model parameters and validation results for *leucoptera, caledonica* and *pycrofti*. Thermocline = thermocline depth; SST=sea surface
444 temperature; Slope = seabed slope angle; Chl = chlorophyll a concentration; SSTad = sea surface temperature absolute deviation around median; SSHD = sea surface height
445 deviation; Wind = wind speed. AUC varies from 0 to 1, with 1 indicating perfect model fit, 0.5 indicating random assignment. Cross validated deviance represents the mean
446 residual deviance per fold across the whole BRT model (lower values denotes better fit, but values cannot be compared between models). Validation deviance indicates the
447 mean residual deviance between the withheld presence and absence values (1 or 0) and model predicted values for those points (higher values denote better model fit). rS
448 indicates Spearman's rank correlation derived from k-fold cross validation of withheld presence points from each model.

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Species	**Number of individuals tracked (total presence points)**	**Parameters (% contribution)**	**# of interactions**	**learning rate**	**# trees**	**Cross validated deviance (internal)**	**Cross validated AUC (internal)**	**Validation deviance (external)**	**Validation AUC (external)**	**rS (P-value) (external)**
Leucoptera	22 (1963)	Thermocline (43.0) SST (22.0) Depth (14.3) log(Slope) (9.1) log(Chl) (8.6) SSHD (3.1)	2	0.0025	1350	0.151	0.765	0.938	0.841	0.9904 (<0.0001)
Caledonica	7 (1102)	SST (36.0) Depth (26.8) log(Chl) (15.7) Thermocline (9.4) SSTad (6.6) SSHD (5.5)	2	0.0025	1800	0.207	0.822	0.671	0.888	0.9880 (<0.0001)
Pycroft	8 (1659)	Depth (33.3) Thermocline (26.7) log(Chl) (14.8) SST (10.4) SSHD (9.6) Wind (5.2)	2	0.0025	4550	0.294	0.829	0.952	0.833	0.9893 (<0.0001)

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Table 4. Activity patterns of *leucoptera*, *caledonica* and *pycrofti* tracked with geolocator-immersion loggers in the tropical Pacific during the nonbreeding period. Flight bouts constitute periods where loggers were dry for ten minutes or longer. Values are the mean ± SD.

	Proportion of time spent on water (%)		Number of flight bouts		Duration of flight bouts (min)	
	Daylight	Darkness	Daylight	Darkness	Daylight	Darkness
leucoptera	75.6 ± 6.5	28.9 ± 17.4	2.0 ± 0.7	5.6 ± 1.4	25.1 ± 5.0	53.6 ± 11.3
caledonica	75.8 ± 4.6	7.9 ± 4.6	1.7 ± 0.5	7.2 ± 0.5	21.7 ± 5.0	67.0 ± 14.2
pycrofti	83.1 ± 11.1	51.0 ± 18.3	2.4 ± 1.5	4.5 ± 1.3	25.8 ± 8.9	45.6 ± 7.9

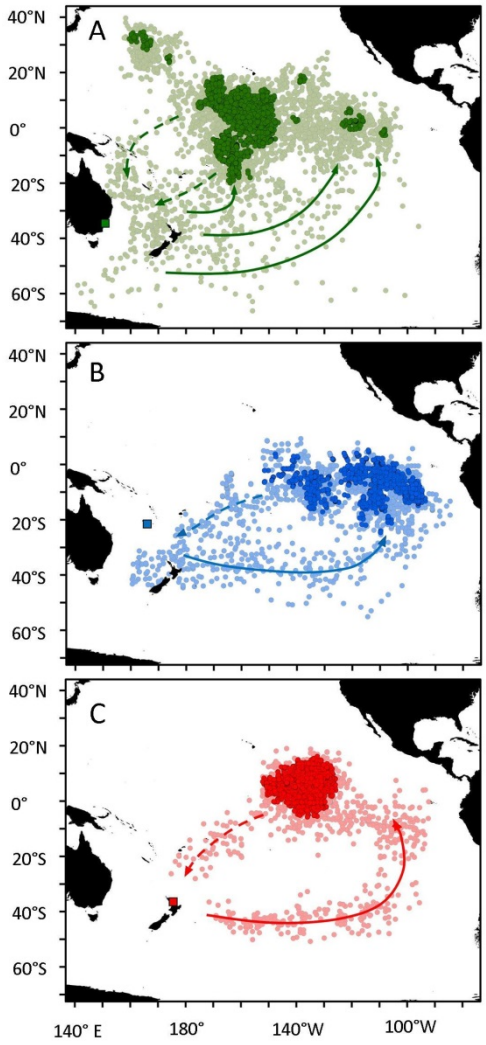

Figure 1 option 1. Locations and general post-breeding (solid lines) and pre-breeding (dashed lines) migration routes of (a) *leucoptera*, (b) *caledonica* and (c) *pycrofti* tracked with geolocators between March and November 2010. Locations shown in bold colour are those that were within monthly 50% kernels during the nonbreeding season (Apr-Oct) and used as presence data in the species distribution models.

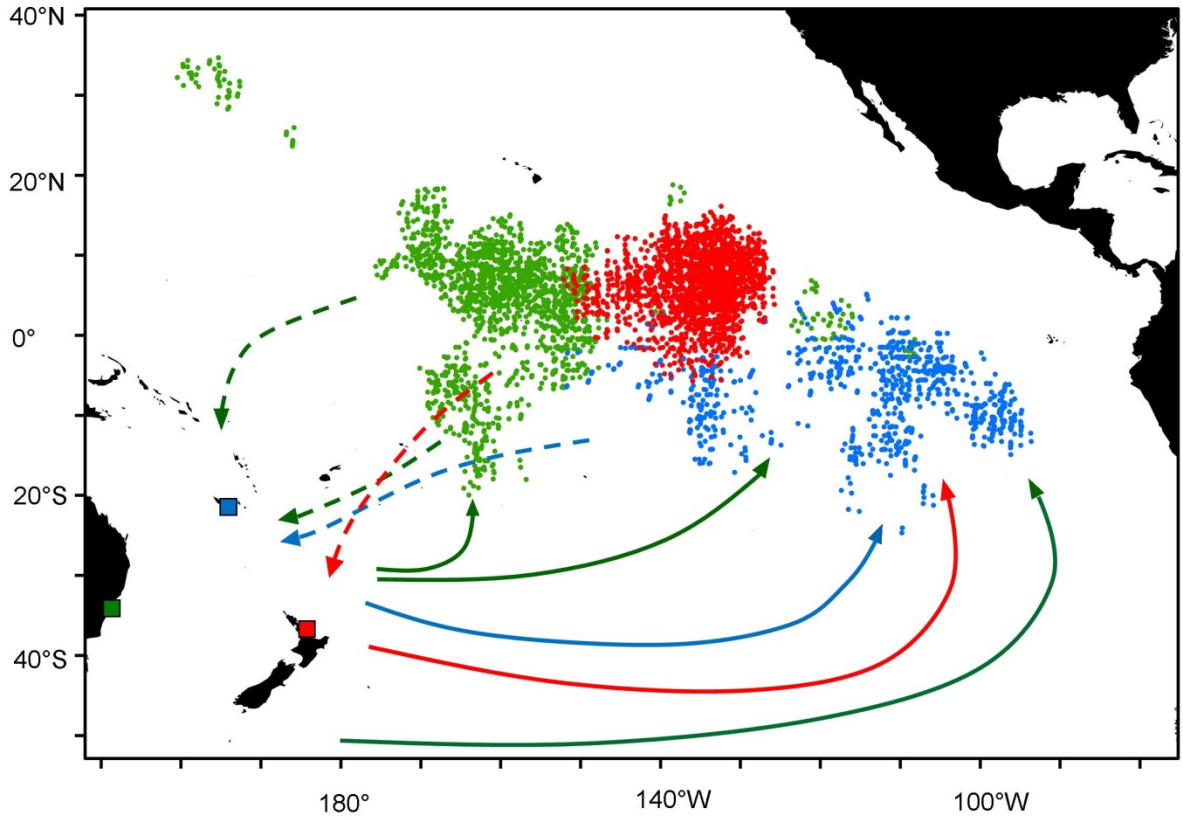

Figure 1 option 2. Locations and general post-breeding (solid lines) and pre-breeding (dashed lines) migration routes of *leucoptera*, (green) *caledonica* (blue) and *pycrofti* (red) tracked with geolocators between March and November 2010. Locations are those that were within monthly 50% kernels during the nonbreeding season (Apr-Oct) and used as presence data in the species distribution models. Respective species colonies shown as squares coloured as above.

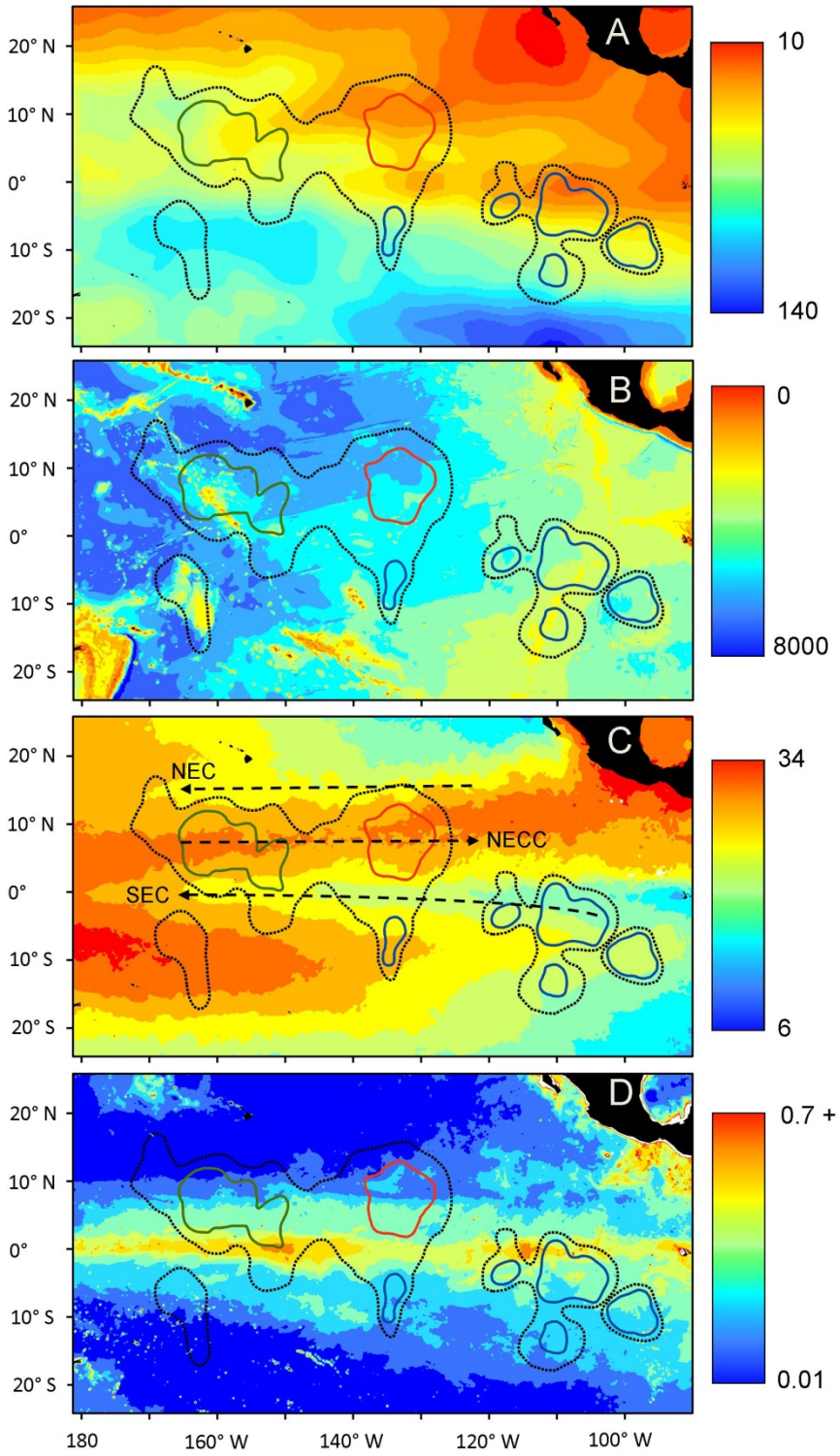

Figure 2. Nonbreeding distribution of *leucoptera*, *caledonica* and *pycrofti* between April and October 2010 overlaid on averaged oceanographic climatologies for the month of July. The 90% (black dashed lines) kernel contours of all species locations and the 50% (coloured solid lines) for each species from April to October: *leucoptera* (green lines), *caledonica* (blue lines) and *pycrofti* (red lines). The environmental layers are ordered by collective contribution to all three species models: A) Thermocline depth (m), B) Depth (m), C) Sea surface temperature (C°) and D) Chlorophyll-a concentration (mg/m^3). Dashed lines represent approximate locations of the North Equatorial Current (NEC), North Equatorial Counter Current (NECC) and South Equatorial Current (SEC) adapted from (Pennington et al. 2006).

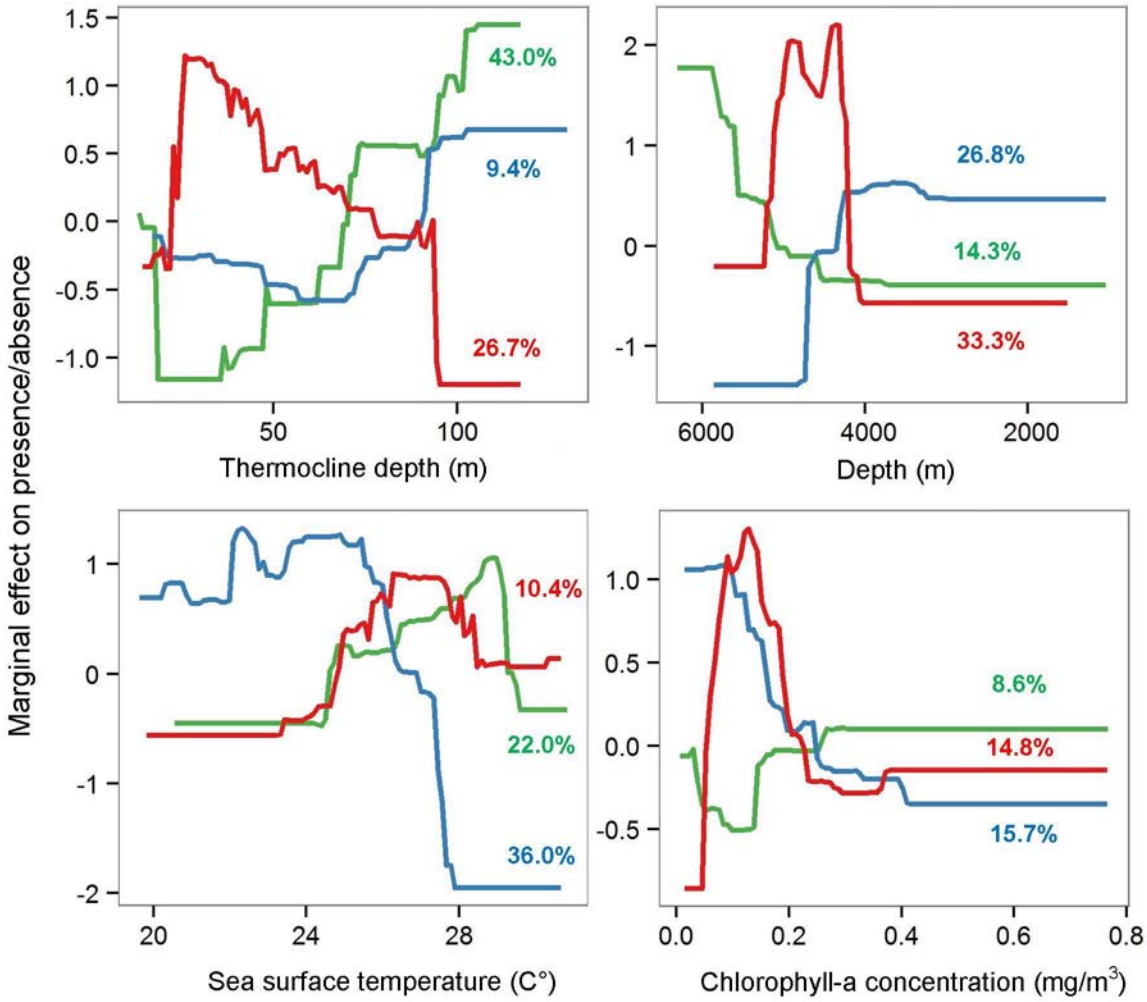

Figure 3.Comparison of fitted functions derived from presence-availability boosted regression tree models of *leucoptera* (green lines), *caledonica* (blue lines) and *pycrofti* (red lines) in relation to the four most influential predictor variables across all taxa. Y axes represent the relative effect of each predictor variable (x axes) on petrel habitat use while fixing all other variables to their mean value. Positive Y-axes values represent a positive contribution by the predictor variable to species presence, and negative values indicate a negative contribution. The percent contribution of each predictor variable to each species model is given by labels in plot, coloured as per species.

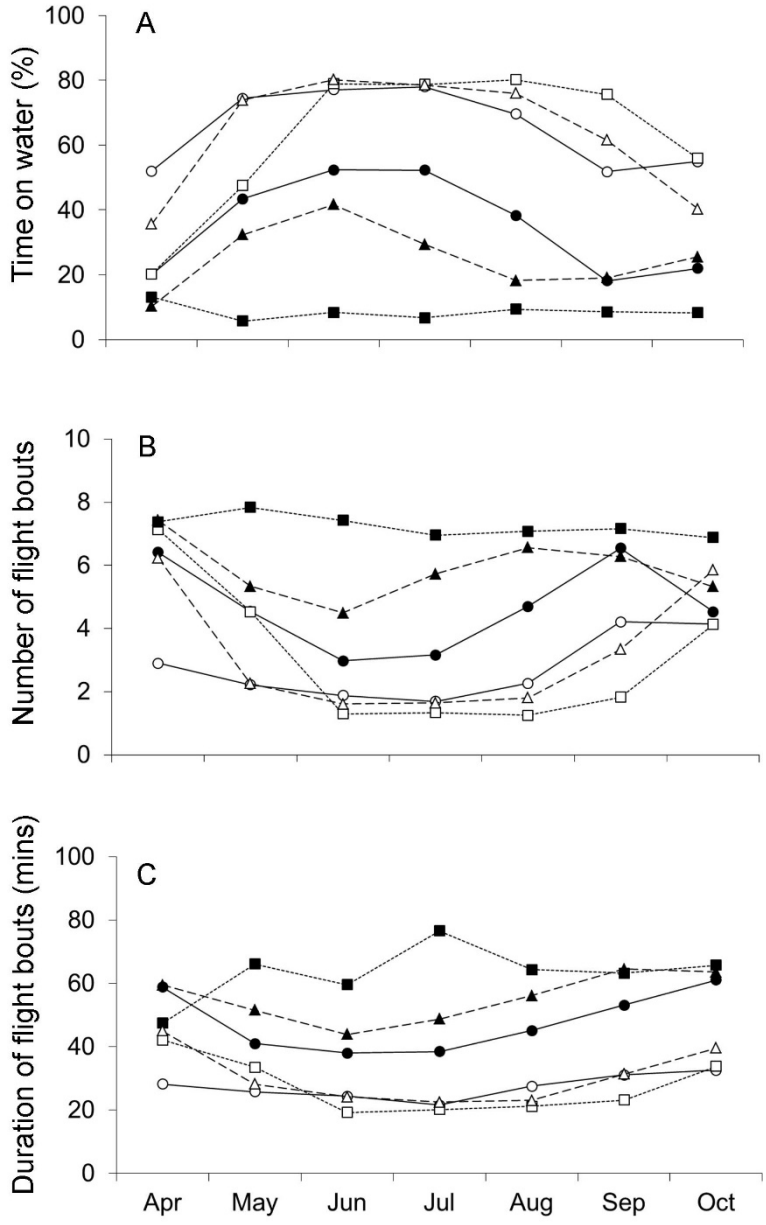

Figure 4. Mean monthly activity metrics during daylight (clear symbols) and darkness (filled symbols) for *leucoptera* (triangles), *caledonica* (squares), and *pycrofti* (circles) tracked with geolocator-immersion loggers during the nonbreeding season including A) Percent of time on water, B) Number of flight bouts and C) Duration of flight bouts.

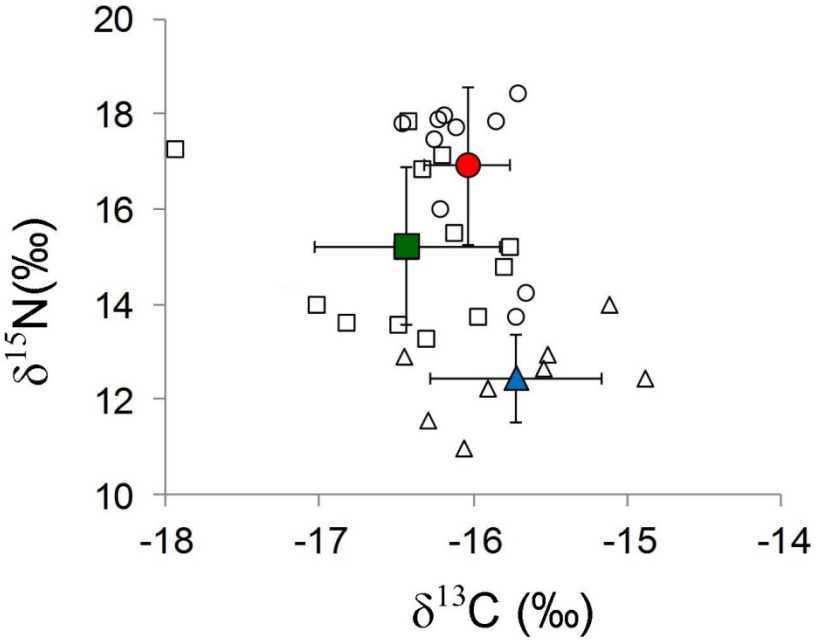

Figure 5. Feather stable isotope ratios of *leucoptera* (green square, n = 12), *caledonica* (blue triangle, n = 7), and *pycrofti* (red circle, n = 10) tracked with geolocator-immersion loggers during the non-breeding season. Coloured symbols and errors are the mean ± s.d., and unfilled symbols correspond to individual values.

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